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BOTANICAL GAZETTE

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BRYOLOGICAL PAPERS

II. THE ORIGIN OF THE CUPULE OF MARCHANTIA CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 120

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(WITH FOURTEEN FIGURES)

The study of the cupule of *Marchantia* has evidently been confined to the later stages of its development, and especially to the origin of the gemmae and the order of cell division in them. Nowhere have we been able to find any account of the origin of the cupule, and the earlier stages of its development seem to have escaped observation. Its homology with other structures in the upper part of the thallus has apparently been a matter of speculation rather than of investigation. Thus, CAMPBELL casually remarks¹ that the gemma cup is apparently a specially developed air chamber, but gives no details and adduces no evidence therefor.

Although *Marchantia* has been much investigated and indeed has been long a favorite subject for instruction in laboratories, KNY seems to have been the first to examine any of the early stages of development of the cupule itself. This he did for the purpose of illustrating the development of *Marchantia* on his charts and describing the same in the accompanying text.² But he does not show or describe the origin of the cupule; the earliest stage referred to corresponds roughly to our *fig. 10*, when it has become a rather deep pit.

Our studies upon the origin of the air chambers in *Marchantiales*³ suggested to us an inquiry into the origin of the cupule, to determine

¹ CAMPBELL, D. H., Mosses and ferns, 2d ed. 44. 1905.

² KNY, L., Wandtafeln. Ser. III, *pl. 84*, text p. 366.

³ BARNES AND LAND, The origin of air chambers. *BOT. GAZETTE* 44:197-213.
1907.

whether it could possibly be homologous with an air chamber. From an a-priori consideration of the general character of the cupule and the air chamber this idea commended itself to us both. The walls of the cup, especially the thin, lobed margin, seemed to correspond very well with the epidermal roof of the air chamber, opened wide instead of having only a narrow orifice. The gemmae, borne upon a single cell arising from the floor of the cup, might well be

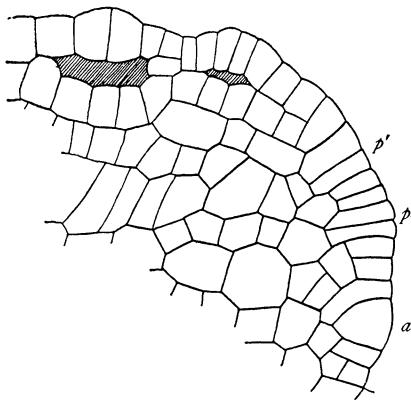


FIG. 1.—Early stage of cupule; p , p' , undivided cells, primordia of two (?) gemmiparous areas; a , apical cell; air chambers shaded.

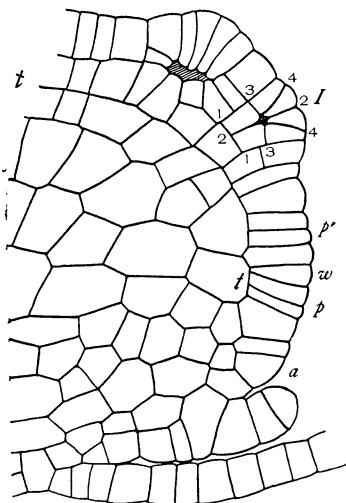


FIG. 2.—Early stage of cupule; p , p' , as in fig. 1; w , probably a rim cell between two gemmiparous areas; a , apical cell; t , t , line showing tissues of thallus involved in a cupule.

only a modified form of the chlorophyllose filaments of the air chamber. So natural and neat did the homology appear, that the brief prior statement of it by CAMPBELL (*l. c.*) was discovered with a distinct sense of disappointment when we began to look into the literature. But evidence for this homology could not be found therein, and against it was to be put the fewness of the cupules, their limitation to the median line, where the air chambers are least developed, and the fact that the gemmiparous region covers many times the area of an air chamber. The matter evidently needed examination. Actual observation of the origin of the cupule speedily dissipated all

notions of its homology with an air chamber, as we now proceed to show.

Abundant fresh material was at hand from thrifty plants of *Marchantia polymorpha*, grown under glass by Mr. JOHN COOK, the skilful gardener of the department, who has taken much pains with the cultivation of Hepaticae. Being transferred directly from the

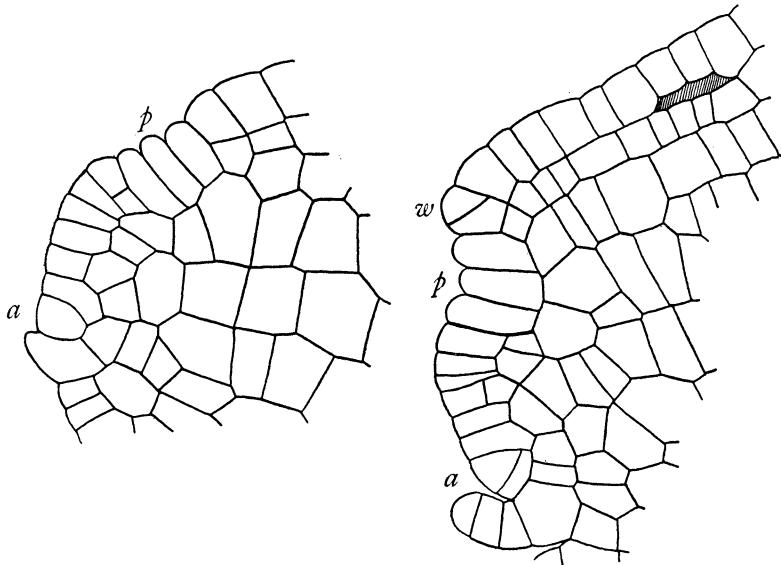


FIG. 3.—Gemmiparous area (*p*) outgrown by adjacent tissues.

FIG. 4.—Stage nearly as in fig. 3; *w*, a rim cell cutting off the primordium of a lobe of the cupule.

cultures to the fixing fluids, the material was in exceptionally good condition.

Our figures show usually only the cell walls, the perfectly preserved contents being omitted for the sake of clearness. Mitotic figures were common, showing that the cells were in active growth. The figures are of longitudinal sections, except fig. 13, are all drawn to the same scale, and having been reduced one-half are now magnified about 625 diameters.

Longitudinal sections through the apex of gemmiferous plants show, as near to the apical cell as the third segment, a differentiation in the cells which are to form the gemmiparous area. Instead of

dividing by several successive periclinal walls, as most of the segments promptly do, the superficial parts remain for some time conspicuously undivided (p , p' , fig. 1), and so are distinguishable by their depth. In particular it is the final periclinal divisions that fail. This will be more evident by following the usual segmentation of the mother cell of an air chamber. In fig. 2, the young air chamber I originated as usual in a cell which underwent one periclinal division,

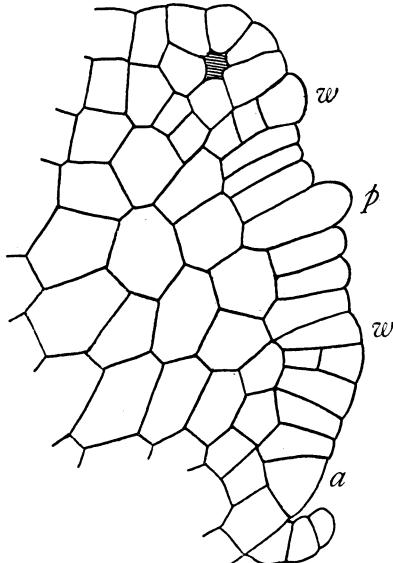


FIG. 5.—Elongation of a single gemmiparous cell (p); w , rim cells, the posterior oldest and most advanced in division.

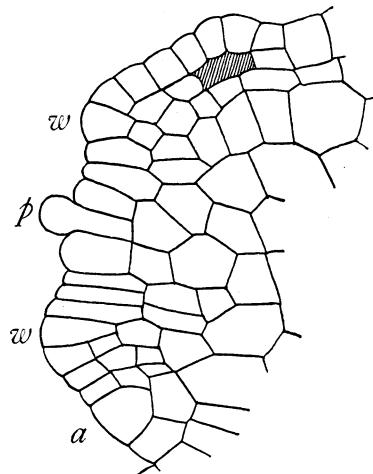


FIG. 6.—A somewhat later stage than fig. 5.

forming the wall 1 , 1 ; then an anticlinal one (2 , 2); these two surface cells each divided periclinally (3 , 3), and cleavage occurred at the junction of walls 2 and 3 . (The curved anticlinal walls, 4 , 4 , succeeded the cleavage.) It is the divisions 1 , 1 , and 3 , 3 , or only the latter, which do not appear in the gemmiparous areas (p , p').

The relative extent of the area which these undivided cells cover, and the occurrence of somewhat different cells (w) between them, make it not unlikely that in figs. 1 and 2 the primordia of two cupules are laid down in close succession; but of this we cannot be sure.

The failure of the gemmiparous cells to divide allows their neigh-

bors to outgrow them, so that they can soon be located by the depression of the surface, as well as by their form and size (p , fig. 3). The depression, however, is not always well marked at this stage (cf. fig. 5). The contents, too, are sometimes distinctive, a glandular appearance being not infrequently noticeable; but as all the cells thereabouts are rich in protoplasm, this feature is not very striking.

The next step in development is the prolongation of one or more

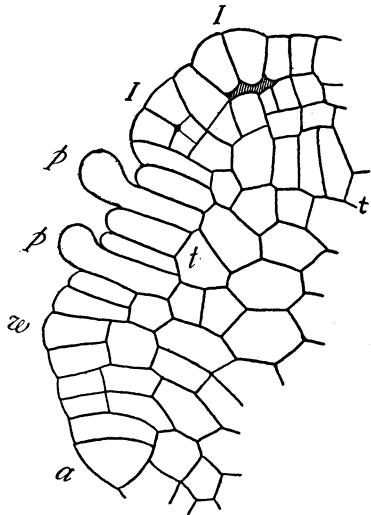


FIG. 7.—Two gemmiparous cells elongated; I , young air chambers; t , t , as in fig. 2.

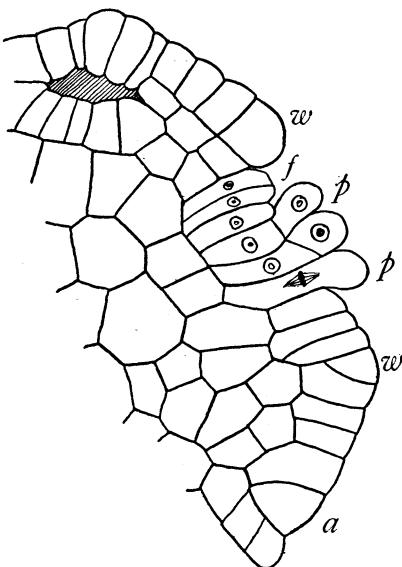


FIG. 8.—Further elongation and first division of gemmiparous cells (p , p); f in f longitudinal division; w , rim cells.

of the gemmiparous cells into papillae (p , figs. 5, 6), and simultaneously the further upgrowth of the cells at the rim of the depression, and first on the posterior margin (w , figs. 4, 5, 6). The free ends of the papillose extensions quickly enlarge (figs. 7, 8) and doubtless secrete some of the mucus in which the whole apical region is enveloped. Certain of the cells that form the rim divide obliquely (w , figs. 4, 8). Probably the cells thus cut off are the primordia of the thin lobes, which are so marked a feature of the mature cupule; for even in this early condition the rim becomes scalloped.

After some further extension and enlargement, the gemmiparous

cells divide transversely (p , p , fig. 8), and soon another division occurs (p , fig. 9), by which three cells are formed, a basal cell (b), a stalk cell (s), and a gemma cell (g). The latter continues to divide in the

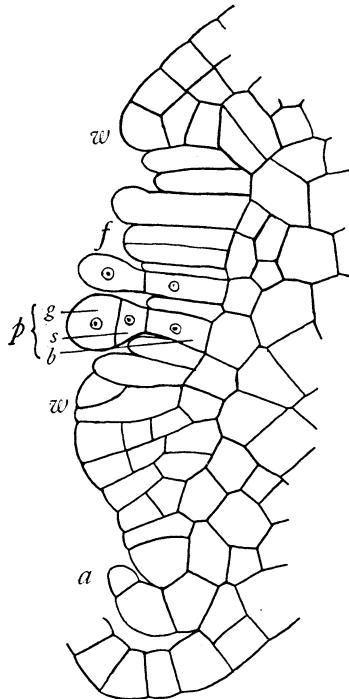


FIG. 9.—Progressing transverse (p) and longitudinal (f) division of gemmiparous cells; the former producing a basal cell (b), a stalk cell (s), and a gemma cell (g).

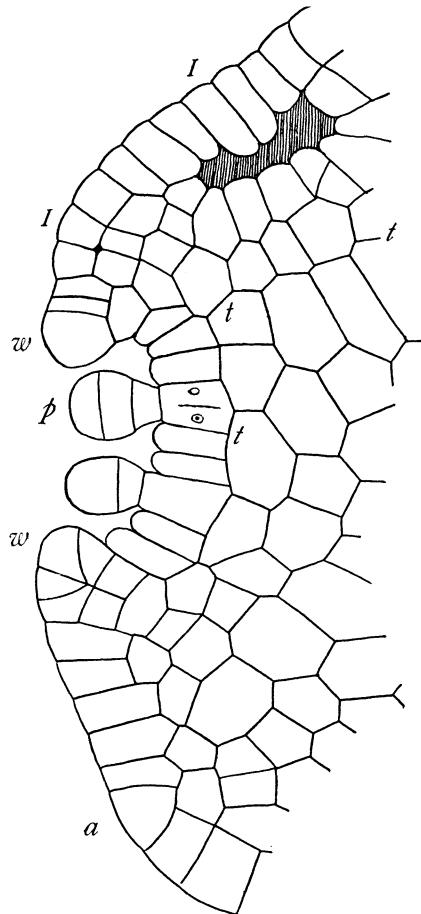


FIG. 10.—Basal cell of p undergoing longitudinal division; w , much further developed and depression deepened; I , young air chamber; t, t, t , shows relation of cupule and air chamber.

fashion frequently described and figured (cf. also figs. 11, 12, 13), and finally produces the gemma. The stalk cell undergoes no further division, but the basal cell divides longitudinally at least once (p , fig. 11). Later it may undergo repeated division, producing new

gemmae, so that each basal cell ultimately becomes the center of a group.

As the primordium of a cupule grows older, the number of gemmiparous cells forming its floor is increased by longitudinal (anticlinal) divisions (*f*, figs. 8, 9). The new floor cells so produced grow into

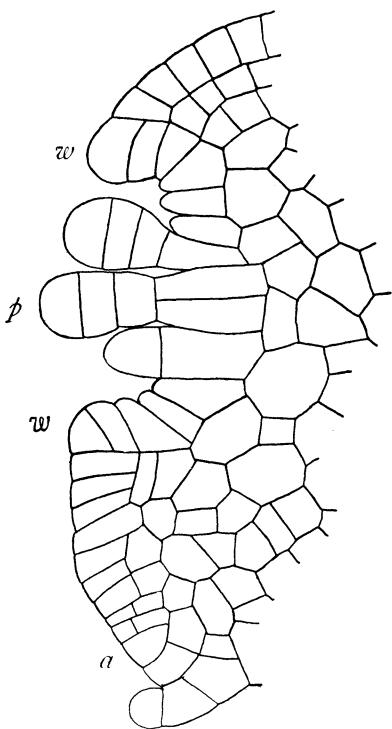


FIG. 11

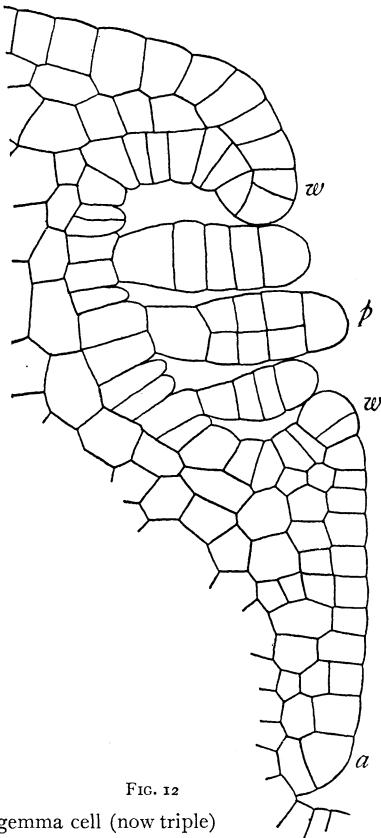


FIG. 12

FIGS. 11, 12.—Further development of gemma cell (now triple) and rim (*w*).

papillae and soon produce gemmae. Thus the gemmiparous area is increased in two ways: by the anticlinal division of the primordial cells, and by a similar division of basal cells that have borne or are bearing gemmae. The tissues adjacent grow rapidly, leaving the floor of the cupule soon far below the general surface (fig. 12), and the rim continues to outgrow the developing gemmae, which are embedded in mucus. The antero-posterior diameter of the young

cupule is less than the transverse diameter, as shown by *figs. 12* and *13*, which represent respectively longitudinal and transverse sections through cupules of about the same age.

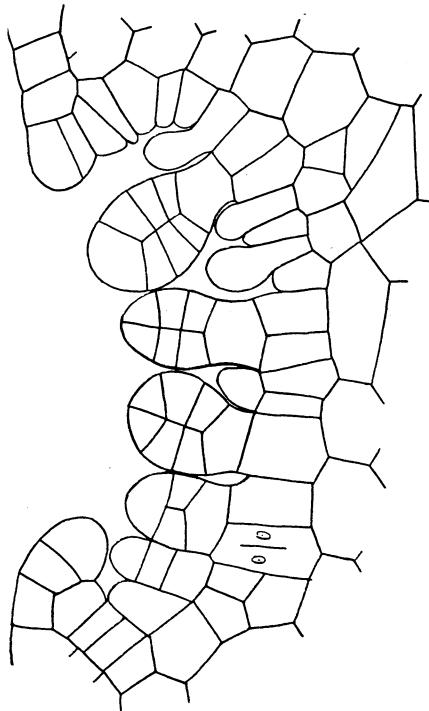


FIG. 13.—Transverse section of a cupule about the same age as *fig. 12*.

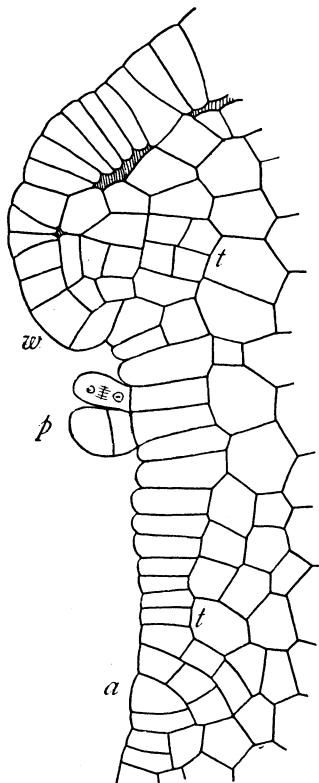


FIG. 14.—Origin of cupule of *Lunularia*; *p*, gemmiparous cells elongated and dividing; rim (*w*) developed only on posterior margin; *I*, young air chamber.

It is not necessary to follow the history of the cupule further, for it is a familiar object in all laboratories of instruction and has been well described.

The cupule of *Lunularia* has also been investigated sufficiently to show that its origin is essentially the same as that of *Marchantia* (*fig. 14*), except that the development of the rim takes place only on the posterior side of the gemmiparous region, which is also far more extensive. In some cases, late in development, a slight anterior

elevation continues the line of the posterior rim and so suggests the circular cup of *Marchantia*.

The superficial origin of the gemmae is thus perfectly clear. They cannot be considered as in any sense homologous with the chlorophyllose filaments of an opened air chamber, nor has the cup any relation to the epidermal roof. The thicker part of it *contains* air chambers, and the thin part is simply a scalelike outgrowth of the epidermis. The difference between an air chamber and a cupule becomes especially striking when a cupule originates near an air chamber, as shown in *figs. 2, 7, 10, 14*, at *I*. Then, although the gemmiparous cells are seen to be superficial, they evidently represent cells that otherwise might produce not only the roof, filaments, and floor of an air chamber, but also a considerable portion of the thallus beneath the air chamber. In *figs. 2, 7, 10*, the line, *t, t*, can be followed clearly, showing how deeply the gemmiparous cells involve the tissues of the thallus. It is not surprising, therefore, that the gemma cup, though of superficial origin, is a depression in the thallus, and that air chambers clothe its sides.

Incidentally we may add that the origin of the gemmiparous cells, as herein shown, precludes our acceptance of GOEBEL's conception that in *Marchantia* the gemmae are homologous with "slime papillae."⁵ The formation of mucus cannot be considered as a special function of any particular cells, though the so-called slime papillae have the name of "secreting" it. In fact young cells of very different origin and fate form mucus, and it is doubtful if any of the younger ones fail to form it. These "papillae" are purely superficial organs, and scarcely agree with the gemmiparous cells in anything except that at one time both project above the surface. How can the latter, which involve so considerable a part of the thallus, corresponding, as above shown, to the whole air chamber region and two or more layers of cells below it, be properly likened to such transient and superficial outgrowths as the "slime papillae"? To pronounce the two homologous throws no real light upon the nature of the gemmae, for the production of which there is such early and striking preparation.

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⁵ GOEBEL, K., "Die Brutknospe von *Marchantia* und *Lunularia* kann auch als einer Schleimpapille homolog betrachten werden." *Archegoniatenstudien XII. Flora* **98**:314. 1908.